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Discussion on the Origin of Vertebrates.

January 20 and February 3, 1910.

BY

Dr. W. H. GASKELL, F.R.S.; Prof. E. W. MacBRIDE, F.R.S.; Prof E. H. STARLING, F.R.S.; Mr. E. S. GOODRICH, F.R.S., F.L.S.; Dr. H. GADOW, F.R.S.; Dr. A. SMITH WOODWARD, F.R.S., F.L.S.; Prof. ARTHUR DENDY, F.R.S., Sec.L.S.; Sir E. RAY LANKESTER, F.R.S., F.L.S.; Dr. P. CHALMERS MITCHELL, F.R.S., F.L.S.; Prof. J. STANLEY GARDINER, F.R.S., F.L.S.; The Rev. T. R. R. STEBBING, F.R.S., F.L.S.; and Dr. D. H. SCOTT, F.R.S., P.L.S.

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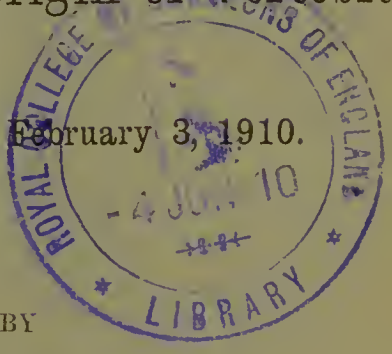

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Dr. D. H. Scott, M.A., F.R.S., President, in the Chair.

In accordance with the announcement from the Chair at the previous Meeting, the Meeting was devoted to a discussion upon the

ORIGIN OF THE VERTEBRATES.

Dr. W. H. Gaskell, F.R.S. (Visitor), who opened the Discussion, said:—I take it for granted that we all believe in Evolution and that an upward progress can be traced from the Protozoa to Man. Now the formation of the Metazoa from the Protozoa and the progress of the Metazoa upwards signifies that the separate units composing the individual have been coordinated for the well-being of that individual. Such coordination has taken place in two ways: (1) a chemical method, by the formation of hormones; (2) a nervous method, by the formation of a central nervous system, and it is self-evident that as soon as a central nervous system is formed, such nervous coordination, especially in connection with the formation of the special senses of sight and smell, must become the important factor in the life of the individual, and its further and further development must constitute the most important factor for the upward progress of the animal race. The first point I want to impress upon you is that for all questions of Evolution, the central nervous system rather than the alimentary canal is the most important factor.

Throughout the whole history of the attempts to find out the origin of Vertebrates one point stands out clearly: whatever other views have been put forward there have always been strong supporters of the view that the Vertebrates have arisen from that great group of segmented Invertebrates, the Appendiculata, and such supporters have not been outsiders of no account, but largely the main authorities in the zoological teaching of the time, *e. g.*, Geoffroy St. Hilaire, Leydig, Newport, Treviranus, Owen, Dohrn, and numerous others, all of whom based their views on the presence of the infundibulum in the Vertebrate in exactly the

same position in the brain as the œsophagus in the Invertebrate group. Supra-infundibular nerve-mass was then the same as the supra-œsophageal, infra-infundibular as infra-œsophageal, and it was seen that the function corresponded marvellously. So powerful was the fetish of the inviolability of the alimentary canal, that no one of these observers ever noticed that if the infundibulum is the old œsophagus, it leads directly into the great cavity of the ventricles of the brain, which again lead into the straight narrow canal of the spinal cord and so through the neurenteric canal to the anus; that in fact if the infundibulum is the œsophagus, the rest of the lining-walls of the cavity of the central nervous system corresponds word for word with the rest of the Invertebrate alimentary canal. On the contrary, they considered the homology could only hold good by turning the animal topsy-turvy and making the back of the Invertebrate correspond to the ventral surface of the Vertebrate. Such a method was doomed to failure and is now universally discredited.

As to the alternative hypothesis of an origin from some non-segmented Invertebrate, please think what it implies and consider seriously whether it is possible to accept it. I imagine we may take it for granted that we know the nature of all the main groups of animals alive on the earth at the present time, and as far as I know the geological record has not brought to light any forms which are not capable of being classified either among or in connection with our present main groups; yet the assumption of this hypothesis is that from some unsegmented animal low down in the scale a group of segmented animals has arisen, in which the alimentary canal was always ventral to the central nervous system and that this group gave origin to the Vertebrate. The absence of any evidence of such chain among living animals at all comparable to the well-marked evidence in the case of the Appendiculata, makes this hypothesis an improbable one; and when the hypothesis further necessitates that not only the central nervous system of such segmented animals has been built up on exactly the same lines as the central nervous system of the Appendiculata, but, contrary to all other nervous systems, has been formed hollow, and that that hollow tube has been formed in such a shape and in such a position with respect to the true nervous elements as exactly to mimic the alimentary canal of the Appendiculata with respect to its central nervous system,—I ask you plainly, does not the improbability amount to an absurdity? This I claim to be the great characteristic of the Vertebrate which differentiates it from all other animals—the presence and nature of this tube around which the central nervous system is grouped: and I beg that those speakers who follow after me and disagree with my conclusions, will give some explanation of the presence and peculiarities of this tube. To me and to all my friends who are accustomed to deal with the Vertebrate central nervous system, the explanation I have given is so self-evident and natural, that it is impossible to look at the matter in any other way.

The paramount importance of the development of the central nervous system for the upward progress of the members of the Animal Kingdom leads to the conclusion that each higher group of animals has arisen in succession from the highest race developed up to that time, by highest meaning the group possessing the best developed central nervous system. This law is proved to us most clearly by the evidence of the rocks in the case of the Vertebrate group.

Thus we see that Man came from the Mammals, the highest race in the Tertiary times. They arose from the Reptiles, the highest race in Mesozoic times, who in their turn arose from the Amphibians, the lords of the Carboniferous epoch. Further back we leave the land and find that the Amphibians arose from the Fishes, the earliest of the Vertebrate race which swarmed in Devonian times. This steady sequence in upward progress from Fishes to Man, revealed by Geology in the long series of ages from the Devonian to recent days, is in absolute conformity with the upward development of brain-power through the Vertebrate series from Fishes to Man, as shown by the investigations of Comparative Anatomists, especially Edinger and Elliot Smith.

If thus it can be proved that such a law of Evolution has held good through the enormous spaces of time between the beginning of the Devonian and the present day, surely it is highly probable that the same law has held throughout, and that therefore the Fishes themselves arose from the race that was the most highly developed at the time when they first appeared: a race therefore which possessed a central nervous system most closely resembling that of the fish.

The evidence of the rocks points to the Silurian age as the time when the Vertebrate first arose, and to the great and striking group of Arthropods which swarmed in the seas at that time, to which the name Palæostraca has been given. These were the highest developed race at that time and from them, according to this law of Evolution, the Vertebrate ought to have sprung.

The great problem then for the study of the origin of Vertebrates resolves itself into this: What was the nature of the earliest fish and of the Palæostraca in Silurian times?

That was the problem I set myself, and it is that comparison which I have attempted organ by organ in my recent book. Such an attempt was rendered possible by the fortunate occurrence of one of the Palæostracan Group—*Limulus* or the King Crab—being still living in the present day, and what is still more important, the remarkable resemblance of *Ammocœtes*—the larval form of the Lamprey—to the fishes belonging to the Osteostraci, especially the close resemblance in position and structure of that remarkable muco-cartilaginous head-shield of *Ammocœtes* to the head-shield of such a fish as *Cephalaspis*.

My object throughout has been by the study of *Ammocœtes* to find out a clue to the past history of these extraordinary early forms of fish. The results are published in my book, and give a

striking evidence of the way in which these early fishes may have arisen from their contemporary Palæostracan rivals. It must always be remembered that these latter animals were not Crustaceans or Arachnids, but the precursors of both of these groups, and much nearer to their origin from the Annelids than the present day Arthropoda. To this circumstance must be attributed the annelid characteristics so markedly found in the Vertebrate, especially in the excretory organs.

It seems to me highly probable that this same law of upward progress, viz., that each successive group has arisen from some member of the highest group existing at the time, holds good also for the vegetable kingdom, especially in view of the statement recently made that Phanerogams arose from Cycads. I hope that the President may see his way to offer a few remarks on that aspect of the question.

The great stumbling block to the acceptance of my theory in the minds of many, is the necessity of making a new digestive tube in a highly organised animal, and yet the same zoologists accept without the slightest difficulty, as a commonplace, the manufacture of a new respiratory organ for breathing air instead of water in the transition from the fish to the amphibian. The previous factor in that case was the swim-bladder which provided the new organ, in the other a respiratory chamber formed by the internal gills; for one of the great characteristics of many members of the Palæostracan group is the absence of external gills and the indication of internally situated gills, and it does seem to me that the evidence is stronger in favour of the Vertebrate alimentary canal being formed from a preexisting respiratory chamber, than that an alimentary canal should have taken on a respiratory function in its anterior end.

The way in which the alimentary canal is innervated by the downgrowth of the great respiratory nerve, the vagus, which is so clearly a segmental nerve for the respiratory part but not for the small intestine, points to this conclusion. The fact that in the well-marked segmental respiratory chamber of *Ammocœtes* a new unsegmented alimentary tube should be formed at transformation, again indicates that a segmented respiratory chamber was the precursor of an alimentary canal. Finally, the position of the anus in such a form as *Drepanaspis* and *Bothriolepis* immediately following upon the region of the head-shield, suggests strongly that in these most ancient and extraordinarily formed fishes the anus followed close upon the mesosomatic or respiratory region just as it does in such an animal as *Limulus*.

Finally in this sketch, not of details but of general principles, I come to the argument that this theory is untenable because it contravenes the fundamental principles of ontogeny.

Against this statement I most strongly protest, for the strength, I might almost say the main strength, of my position is based on the facts of Vertebrate development.

The one great principle of ontogeny is the Law of Recapitulation,

the law which lays down that the past phylogenetic stages which have led to the evolution of any individual are indicated to some extent in the ontogeny of that individual.

This law is confirmed and indicated in a most amazing way by my theory. The theory asserts that the clue to the origin of Vertebrates is to be found in the tubular nature of the central nervous system of the Vertebrate in that the central nervous system is in reality formed of two things: (1) a central nervous system of the Arthropod type, and (2) an epithelial tube in the position of the alimentary canal of the Arthropod.

Is it possible for embryology to recapitulate such a phylogenetic history more clearly than is here the case? In order to avoid all possibility of our mistaking the clues, the nerve-tube in the embryo always opens into the anus at its posterior end, while in the larval *Amphioxus* it is actually still open to the exterior at its anterior end. Consider the shape of the nerve-tube when first formed in the Vertebrate. At the cephalic end a simple bulged-out tube with two simple anterior diverticula, which passes into a narrow straight spinal tube; from this large cephalic bulging a narrow diverticulum, the infundibulum, passes to the ventral surface of the forming brain. This tube is the embryological expression of the simple dilated cephalic stomach, with its ventral œsophagus and two anterior diverticula, which opens into the straight intestine of the arthropod. Nay more, by its very shape and the invariable presence of two anterior diverticula, it points not only to an Arthropod ancestry but to a descent from a particular group of primitive Arthropods. Then comes the formation of the cerebral vesicles and the formation of the optic cup, telling us, as plainly as can be, how the invasion of nervous material over this simple cephalic stomach and its diverticula has altered the shape of the original tube and more and more enclosed it with nervous elements.

So, too, in the spinal cord region. When the tube is first formed, it is a large tube, the latero-ventral part of which presents two marked bulgings; connecting these two bulgings is the anterior commissure. These two lateral bulgings, with their transverse commissure, represent with marked fidelity the ventral ganglion masses of the Arthropod with their transverse commissure, and occupy the same position with respect to the spinal tube, as the ganglion-masses do with respect to the intestine in the Arthropod. Then the further development shows how, by the subsequent growth of the nervous material, the calibre of the tube is diminished in size and the spinal cord is formed.

Again, I say, is it possible to conceive that embryology should indicate the nature of the origin of the Vertebrate nervous system more clearly than it does?

It is the same with all the other organs. Take for example the skeletal tissues. The study of the Vertebrate embryo asserts that the cartilaginous skeleton arose as simple branchial bars and a simple cranio-facial skeleton, and also that the parenchymatous

variety of cartilage represents the embryonic form. Word for word, the early embryonic stage of the Vertebrate skeleton closely resembles the stage reached in the Arthropod, as shown by *Limulus*, and again records unmistakably the past history of the Vertebrate.

So, too, with the whole of the prosomatic region; the situation of the old mouth, the manner in which the nose of the Cephalaspidian fishes arose from the Palæostracan, are all shown with vivid clearness by Kupffer's investigations of the early stage of *Ammocœtes*, while at the same time the closure of the oral cavity by the septum shows how the oral chamber was originally bounded by the operculum. Nay, further, the very formation of this chamber embryologically was brought about by the forward growth of the lower lip, just as it must have been if the chilaria grew forward to form the metastoma. So, too, the study of the embryo teaches that the branchiæ arise as ingrowths, that the heart arises as two longitudinal veins, just as the theory supposes from the facts provided by *Limulus* and the Scorpions.

No indication of the origin of the thyroid gland is given by the study of its structure in any adult Vertebrate, but in the larval form of the Lamprey there is still preserved for us a most graphic record of its past history.

The close comparison which it is possible to make between the eye-muscles of the Vertebrate and the recti muscles of the Scorpion group on the one hand, and between the pituitary and coxal glands on the other, are based upon, or at all events are strikingly confirmed by, the study of the cœlomic cavities and the origin of these muscles in the two groups. In fact the embryological evidence of the double segmentation in the head and the whole nature of the cranial segments, is one of the main foundation stones on which the whole of my theory rests.

So it is throughout. Turn to the excretory organs: it is not the kidney of the adult animal which leads direct to the excretory organs of the primitive Arthropod, but the early embryonic origin of that kidney.

So far from having put forward a theory which runs counter to the principles of embryology, I claim to have vindicated the great Law of Recapitulation which is the foundation stone of embryological principles. My theory is largely based upon embryological facts, and its strength consists in the manner in which it links together into one harmonious whole the facts of Embryology, Palæontology, Anatomy, and Physiology.

It cannot then be said that my theory contravenes this great law of development, the Law of Recapitulation. What, then, is the objection? It is that it disregards the germ-layer theory, a theory which assumes that the origin of the Metazoa from the Protozoa took place by the formation of a gastrula-form—Haeckel's hypothetical Gastræa—which gave a fixed and definite morphological origin to hypoblast, and that from that time up to the latest animal development that hypoblastic layer has always

remained the same. Such a positive assertion, if true, immediately puts out of court any theory which forms an alimentary canal out of something which is not hypoblast. It makes the alimentary canal the keystone of the whole fabric of Evolution, not the central nervous system.

As I have pointed out in my book, the evidence of Brehm and others is to the effect that there is no such morphological criterion of hypoblast, but, on the contrary, the hypoblast is a physiological conception rather than a morphological one, being the term given to that layer which is found by its development to form the digestive tube of the animal, and that in the earliest members of the Metazoa, where we ought to expect the gastrula formation to be most conspicuous, there it is most conspicuously absent, while it is most clearly evident in those free-living pelagic blastula-forms in which, owing to the absence of yolk, the necessity exists of obtaining food from the outside even from the early blastula stage.

According to the Law of Recapitulation we may expect to find in the developmental history of the Metazoa some indication of the nature of the Protozoan ancestor which gave origin to the Metazoa. Such indication is given with absolute uniformity in all the Metazoa by the blastula stage, not by the so-called gastrula stage. The blastula represents one of the highest Protozoan forms, such, for example, as *Volvox*, as I have suggested in my book, and the blastula stage affords yet another indication of the great law, that the upward progress of the Animal Race has always been brought about by the genesis of the next highest form from a member of the highest existing group of animals.

Prof. E. W. MacBride, F.R.S. (Visitor), remarked:—

Dr. Gaskell has given us a brilliant exposition of his famous theory of the "Origin of Vertebrates" to which it is impossible to reply at all adequately in a quarter of an hour. Fourteen years ago this theory was presented to the Cambridge Philosophical Society and I then gave expression to many objections which I felt to it; and I confess that those objections remain in unaltered force to-day. Not one of them has been removed by Dr. Gaskell's speech, nor has a perusal of the latest edition of his book weakened one of them in the slightest degree.

The first and most fundamental objection is to the whole nature of Dr. Gaskell's morphological reasoning. Unless this kind of reasoning is to be guided by definite rules it becomes a mere arena for the display of the imaginative faculties. The change which one man regards as inconceivable another thinks the most natural in the world. I, for instance, cannot contemplate in cold blood a free-living animal giving up its alimentary canal and beginning to digest with its skin, whilst to Dr. Gaskell this seems the most natural transition in the world. But what rules for morphological reasoning are suggested? Tacitly or avowedly, all zoologists agree on this—morphological reasoning must conform to precedent. But what constitutes precedent in this case?

Those changes about the nature of which all zoologists are agreed, such as the relationship of an aberrant genus to the typical form of the family or order to which it belongs. Thus no one doubts that the Hermit Crab is descended from a normal Lobster or *Chætopterus* from a normal Annelid. The changes involved in the descent of such forms from the more normal types give us the only rules we can have to guide us when we attempt the more difficult task of passing from one phylum to another.

Now Dr. Gaskell, in assuming that Vertebrates are descended from some Palæostracan type of Arthropod of which the only survivor is *Limulus*, is obliged to reconstruct the entire animal, leaving only the central nervous system standing. We are asked to believe that the original alimentary canal has become the neural canal, and that a new alimentary canal has developed from the skin of the ventral surface of the body. No precedent for such a change can be gathered from any of the data I have mentioned above.

Again, the skin of the lower Vertebrates is ciliated, and this is most undoubtedly a primitive condition seeing how widely it is spread amongst the lower groups in the Animal Kingdom. No Arthropod * is ciliated at any time of its existence: its whole organisation is dominated by the tendency to form thick chitinous cuticle. We have to suppose that this tendency, which is spread throughout Arthropoda from the highest to the lowest, has been overcome and that a reversion to a primitive soft ciliated ectoderm has been accomplished. No precedent for such a change can be gathered from the entire Animal Kingdom. It is no answer to this to show that in *Ammocœtes* and one or two other cases a thin exterior cuticle is developed on certain parts of the skin—for it is the normal sequence of things that a cuticle should succeed to a ciliated skin as a secondary change, but the change in the reverse direction is absolutely without precedent.

The eyes of Vertebrates, or, to speak more correctly, their retinæ, are lateral pockets of the walls of the neural canal—which we are told to regard as the old alimentary canal. The eyes of Arthropoda are, without exception, modifications of the external skin. Are the lateral eyes of the two groups homologous or are they not? If they are homologous, how is their different origin explained? Dr. Gaskell figures a section of *Artemia* in which one of the liver saccules is in close contact with the lower layer of the eye. He hints that perhaps part of the eye is developed from the epithelium of the liver saccule, but this is in flat contradiction to the work of every zoologist who has examined their development. If the eyes in the two cases are not homologous, why did the Arachnid ancestor of Vertebrates give up its external eyes and develop a new pair from its old alimentary canal? To say that there is no precedent for such a change is to put it mildly.

* I hardly think it necessary to refer to the ciliation of the genital ducts of *Peripatus*, the only exception to this rule, since *Peripatus* is hardly as yet an Arthropod.

Dr. Gaskell indulges in a polemic against the germ-layer theory, whilst maintaining strongly the theory that the development of the embryo recapitulates the history of the race. He seems to be unaware that the germ-layer theory is only a special instance of the recapitulation theory. It asserts that the egg in its progress to a hollow blastula recapitulates the change from a unicellular to a multicellular Protozoon. This part of it Dr. Gaskell accepts, and with justice, for in the development of simple and primitive types the blastula crops up throughout the entire Animal Kingdom. But in every case which is free from the complication of yolk, the blastula is transformed into a hollow gastrula by a process of invagination, so that we find that in the Arthropod *Lucifer* and the Vertebrate *Amphioxus* the process is very similar. And yet Dr. Gaskell asks us to believe that in the one case the cavity is homologous with the neural canal of Vertebrata and in the other with the gut! Such reasoning seems to me to be very difficult to accept. Dr. Gaskell assumes that *Lucifer* developed the hollow gastrula stage because its egg is a small one floating in water and has to absorb nourishment early through the blastopore, but the fact is that in this stage of its development the egg of *Lucifer* is in a tough shell and that before it begins to absorb nourishment the blastopore closes, and this is the case with *Amphioxus* also. The doubts as to the validity of the germ-layer theory have concerned themselves chiefly with the nature of the third layer, the mesoderm. If everything which is found between ectoderm and endoderm be called mesoderm no doubt confusion will arise, for heterogeneous structures are confounded under this name. But the more careful investigation of doubtful cases in recent years, for which we are specially indebted to the Americans, have shown that if by mesoderm we mean the *wall of the cœlom*, then this is homologous in all cases and always arises from the gut-wall.

I pass over minor difficulties of Dr. Gaskell's theory, such as the degeneration of the ancient genital gland into packing tissue surrounding the brain, and the transformation of the womb into a gland which in *Ammocœtes*, as in *Amphioxus*, produces a string of mucus to entangle food; for the mind which accepts the main ideas of the theory will be capable of digesting such trifles also. We come then to the only points in Dr. Gaskell's theory which in the mind of any zoologist would constitute even *prima facie* evidence in its favour, viz. the external resemblance between some of the armoured fish of the Devonian and the contemporary Eurypterids, coupled with the assertion that when Vertebrates appeared Arthropods were dominant in the water, and that only creatures with strong armour and well-developed nervous systems could have overcome them. Dr. Gaskell infers that if the primitive Vertebrates had been like *Amphioxus* they never could have won the day. Now to this, two answers may be made. First, that the resemblance is purely superficial, in fact far less than exists between a Whale and a Fish: we should in fact have far more reason for classing Whales as Fish than for regarding *Cephalaspis* as allied

to *Limulus*. This point I shall leave for elaboration to the palæontologists who follow me. Secondly, Dr. Gaskell has no right to assume that *Cephalaspis*-like forms were the first Vertebrates. It is entirely to ignore all that Darwin taught on the imperfection of the geological record, and already the discovery of forms like *Thelodus* with a skeleton of isolated denticles and of fusiform fish like *Birkenia* and *Lasanius*, in which the skeleton, if any, was formed of small isolated plates, has given the lie to such assumptions. If early Vertebrates were like *Amphioxus* they may have existed from Pre-Cambrian times and we should have found no trace of them. Moreover, the form of *Cephalaspis* and its allies is totally unlike the typical fish form. This is fusiform and flattened in the vertical plane, while *Limulus*, like all Palæostraca and the overwhelming majority of Arthropoda, is flattened in the horizontal plane. *Cephalaspis* in outer form resembles such modern fish as *Lophius* (the Angler) and the Gurnards, which habitually squat on the bottom and some of which bury themselves in the mud; and some of these forms actually develop their scales into plates and have their eyes shifted dorsally. I have no doubt at all that whilst *Cephalaspis*, *Pterichthys*, and their congeners were practising this sluggish mode of life, the real ancestors of the dominant Vertebrates of the sea were ranging like flashes of living light through the waters above. It is customary to speak of *Amphioxus* as a degraded creature, but no one who has ever seen it swim will fail to realize the immeasurable superiority of the Vertebrate motor system over that of the Arachnid. The comparison of the one to the screw of a steamer and of the other to an eight-oared boat gives some idea of the difference. We may add that the whole course of evolution in fish and other Vertebrates has tended in the direction of getting rid of external armour, and there is no foundation for Dr. Gaskell's assumption that the possession of heavy external armour indicates a "dominant" form. It really indicates a sluggish form. But Dr. Gaskell continues, there is the unique feature that the Vertebrate nervous system is tubular and that the ganglion cells bear the same relationship to this tube as do the gangha of an Arthropod to its alimentary canal, and the central nervous system is the most important organ in the body: whilst all else may change it *endures*. Here again every single item of this statement may be met with a denial. A tubular nervous system is not confined to the Vertebrata. It is found amongst the Echinodermata in Ophiuroidea, Echinoidea, and Holothuroidea, and in all cases it is formed precisely as in *Amphioxus*. An exposed plate of nervous ectoderm, such as is found throughout life in Asteroidea, is covered by the meeting of two thin non-nervous flaps. Then again the ganglionated character of the nervous system of an Arthropod is appealed to as a sign of high differentiation—but this is entirely to misread it. This character depends on the nature of the locomotor system, which consists of discrete groups of muscles confined to appendages, which leads to a local grouping

of motor nerve-cells. What intelligence *Limulus* has is confined to its minute archicerebrum, and this is probably small in amount. *Amphioxus* has no particular reason to fear *Limulus* on the ground of brains. In the Vertebrate the swellings of the nervous system are associated with the development of large sense organs, but its locomotor organs are the almost continuous bands of muscle known as myotomes, and hence the motor nerve-cells form a practically continuous plate. Moreover, the whole study of the Animal Kingdom is dead against the assumption that all else may change but the nervous system must endure. If we start with the most highly developed Arthropoda, or with the most highly developed Mollusca, we find as we pass back to more primitive forms that the nervous system evaporates into a mist of general ciliated nervous ectoderm. Out of this, as required by the exigencies of motor and sensory organs, accumulations of nerve-cells develop, and disappear with the disappearance of these organs. Of course, like every other organ, when they have persisted for a long time in a phylum they become stable, but why we should trace the highly developed brain of a Cuttlefish back to primitive ectoderm and pass from the developed nervous system of a typical Arthropod to the typical nervous system of a developed Vertebrate—ignoring all the really primitive forms belonging to the Vertebrates, is conceivable to no one who really knows zoology.

The alternative theory to his, as Dr. Gaskell admits, is that Vertebrates arose from some simple form with undifferentiated organs. *Amphioxus* gives us an idea of the Vertebrate structure in its most undifferentiated form, but showing the characteristic Vertebrate organs of notochord, gill-slits and tubular nerve-cord. The worm-like *Balanoglossus* and its allies show the same structures, but without the segmentation characteristic of the muscles of *Amphioxus* and other Vertebrates. But in its development, which shows far more primitive features than that of any known Arthropod, *Amphioxus* resembles *Balanoglossus*. The larva of *Balanoglossus* resembles that of Echinoderms, and here we have a hint of a wide ranging free-swimming group of pelagic animals, the direct descendants of whom are Vertebrata, but the degenerate off-shoots of which at various levels are Echinodermata, Enteropneusta, *Amphioxus*, and Ascidians.

Dr. Gaskell heaps scorn on the idea that Vertebrates, the dominant class, arose from a degenerate like *Balanoglossus*, and asks how such worms could have competed with the big Arthropods. No one supposes that Vertebrates are descended from *Balanoglossus*, but at the immensely remote period of time when the ancestors of *Balanoglossus*, leaving their closely allied compeers the ancestors of Vertebrata, deserted the surface to seek the mud, the ancestors of the Gaskellian Arthropods were probably in the condition of the Trochophore larva.

Dr. Gaskell alludes to Spengel's work on *Balanoglossus* as destroying the supposed Vertebrate character. Nothing could be more mistaken. Every argument of Spengel has been

pulverized, and every statement of Bateson confirmed in the sixteen years that have succeeded the publication of Spengel's work.

Dr. Gaskell calls the theory of "parallel development," by which he means the theory of the independent origin of the great phyla Arthropoda, Mollusca, Vertebrata, &c. from simple forms, an "unscientific and inconceivable suggestion." Surely he has forgotten the 'Origin of Species.'

Does he forget that Darwin felt the differences between these phyla so strongly that he doubted their common origin, and seems to have imagined that they might have originated independently from primordial protoplasm. Does not Dr. Gaskell know that those who give their lives to the study of Zoology have "parallel development" or fan-like development forced on them at every turn, in every section and sub-section of the Animal Kingdom. That the air-breathing type of gastropod Mollusc, for instance, must have originated at least half a dozen times and the snake-like Vertebrate at least a dozen times each time in entire independence of every other. And why unscientific? If protoplasm be fundamentally the same sort of thing at bottom, and if variations be due to definite changes in its chemical composition produced directly or indirectly by changes in the environment, should not like causes have like results?

Dr. Gaskell states that his theory strikes at the root of the conception of parallel development. In this case I venture to predict that the root will prove to be more resistant than the axe with which it is struck.

Prof. E. H. Starling, F.R.S. (Visitor), followed and remarked:

I do not know how far an apology may be considered necessary for the intervention of a physiologist in the discussion of a topic which has hitherto been regarded as the special preserve of the zoologist and comparative anatomist. I understand, however, that the chief criticism of the theory, which has been so ably put before us this evening, has had reference to the method by which the problem is attacked, rather than to the facts in comparative anatomy which have been discovered or collated by Dr. Gaskell. On this point, namely, the principles which must guide any research into the phylogeny of our race, a physiologist has as good a right to be heard as has a comparative anatomist. In fact, it was the author of the 'Origin of Species' himself who introduced physiological considerations into the theory of descent. Darwin showed that the grouping of living beings made by zoologists had a far deeper significance than mere resemblance of form, and were really expressions of blood relationships among the members of any group or between allied groups. He thus replaced a purely conceptual anatomical grouping by an actual physiological kinship. Since the varying degrees of divergence among different forms are to be referred to the survival only of such individuals as are most

fitly adapted to their environment, the problems of relationship, of descent and, in short, of the origin of species become part of that great study of adaptation which is the proper occupation of the physiologist. These problems are bound up, not with the outward seeming of an organ or organs, but with their *use* to the animal in the struggle for existence, and are therefore in the first place problems of function.

In a search for the ancestry of Man and of Vertebrates generally we must therefore remember that we are dealing, not with museum specimens, but with living organisms, and must endeavour to learn what are the essential factors in the life of the animal that give it an advantage over its fellows and tend to the perpetuation of its stock.

We have really two questions to deal with, namely :—

(1) What determines survival of type ? and,
(2) What determines dominance of type ?

Survival is merely a question of perfection of adaptation and does not necessarily imply that the type which survives becomes dominant. There are many holes and corners on the surface of the globe where the environment is of a very special character, and in each of these we shall find some group of organisms adapted for this environment and for none other. In many cases such an environment is furnished by the surface or interior of some other type leading a more active existence. It is in this parasitic condition that we get the most extreme degree of specialized adaptation associated with degeneration of all parts rendered unnecessary by the restricted range of environmental events to which the organism is liable.

Dominance of a type, on the other hand, involves wide distribution and, in most cases, the existence of numerous species of the same general characteristics under widely different conditions of environment. To such a dominant type belongs the Vertebrate with its highest representative, Man. There can be no doubt that the evolution of such a type must have been continuous and progressive. It has often been imagined that the evolution of the dominant forms of life was simultaneous and not successive, and was to be compared rather to the spokes of a fan than to a tree with its branches diverging from a common stem. Such a fan-like evolution could only occur with a complete separation of environments. It is as difficult to conceive that the Vertebrate was evolved from a primitive worm-like organism which shot up past the more highly developed Arthropoda, as it is to believe that mankind is destined to be replaced by some beast that is now being evolved from lower groups in the depths of the sea. But what do we mean by speaking of lower and higher groups ? The idea involved in this antithesis is the same as that included in the term "dominance." The position of any type in the animal scale, the question whether it is to win in life's struggle, is determined

by *range of adaptation* or of reaction. The organ or system on which the range of adaptation depends is the one on which we must concentrate our attention in tracing back the evolution of the Vertebrate. This organ is the central nervous system. There has been no continuous rise in type of the muscular, digestive, or respiratory systems. It is the central nervous system which determines dominance of any type, and the nervous system is the only part of the body which undergoes continuous evolution from the lowest to the highest forms. The reactions of the highest animals are determined by the nerve-cells and tracts laid down in the embryo and inherited from the parents, no new formation or repair being possible after the earliest stages of fœtal life, if indeed at any time. In no case, so far as I am aware, do we find the central nervous system cleared away and laid down afresh in the metamorphosis of an animal. At various times an animal may breathe by its skin, by gills or by lungs. It may digest its food by means of glands derived from the epiblast or hypoblast, and indeed digestive ferments may be produced by almost any cell in the body. It may excrete waste products by kidneys, intestines, or skin; but the central nervous system remains the one unchangeable organ, whose function, namely, the determination of adapted reactions and therefore of survival, cannot be replaced by the vicarious activity of any other part of the body.

Looking back as physiologists we may indeed see that all the main epochs in the evolution of higher forms of life are characterized by changes in the nervous system. The first step was taken when the individuals of a cell colony remained in structural connection, so that the *consensus partium* could be maintained by the propagation of molecular changes along the protoplasmic strands between the different cells and no longer depended solely on the diffusion into the surrounding medium of chemical substances which might affect friend or foe alike. By a differentiation among these connecting strands a diffuse nervous system was formed with immensely enhanced rapidity of reaction of the whole organism to environmental changes at any part of its surface. The location of the mouth at the front end of the body, *i. e.* the one which in the actively moving animal was first exposed to changes in the environment, was attended by the concentration at this end of the specialized projicient organs of sense, *i. e.* those whose activity was aroused by changes occurring at some distance from the animal, in a region with which a continuation of the forward progression of the animal would bring it in more intimate relations. The presence of these *foreseeing* organs at the anterior end necessarily brought in its train a subjection of all other parts of the nervous system to that part, the supra-œsophageal ganglion, which was the first recipient of the afferent impressions from these organs. The rise in type, which has culminated in the production of Man himself, has been determined simply by a continuous

advance in the complexity of adaptations, and by an increase in the powers of control and foresight exercised by the foremost part of the central nervous system. On these two factors, foresight and control, depends a man's position among his fellows, and a continuous growth in the same factors marks the progression of living forms from the Worm to the highest Vertebrate.

Since the functions which determine survival are those bound up almost exclusively with the central nervous system, this system is taken by Gaskell as his guide in tracing the genealogy of the Vertebrate. I am not sufficiently equipped to bear testimony in favour or otherwise of the facts adduced by Gaskell in support of his theory. I am convinced, however, that the principles on which he has proceeded are the only ones which will lead to a solution of the problem, and that researches along these lines will throw light on the meaning and physiological significance of many organs whose part in the economy of the body is still a mystery. It is difficult to understand the attitude which has been taken up by the majority of zoologists towards this theory of the origin of Vertebrates. We find zoologists themselves putting forward theories of the descent of Vertebrates based on a more or less profound study of all sorts of organs and structures which really have little or no importance in the life of the animal, or can be replaced vicariously or structurally with the utmost ease. Thus they concentrate their attention on organs such as the alimentary canal, blood vessels, fœtal membranes, excretory organs, the notochord, but pay little or no regard to the one system of the body which is all-important in determining the continuous series of adaptations which make up the life of the animal. And what is strange is that in most cases no palæontological evidence seems to be brought forward in favour of these hypotheses. I do not know whether succeeding speakers will be able to adduce any facts from the geological record in favour of the existence of the strange slug-like animals, with or without holes punched in them, which have been evolved out of the inner consciences of our most distinguished zoologists and assigned to us as our remote ancestors. To an onlooker like myself the striking resemblance between the earliest fishes and the Arthropoda which were the dominant type just before the appearance of these Vertebrates, is striking evidence in favour of Gaskell's theory. I would ask the morphologists present here to-night to explain how they account for this striking similarity. If the gastrula theory had been mentioned in the first chapter of Genesis, it is possible that the presence of those earliest fishes in the earth's crust might be regarded as a divinely appointed trial of faith for the orthodox among zoologists. It seems to me that the morphologist, while professing a lip service to the doctrine of Evolution, has really forsaken the teachings of Darwin and gone back to the worship of his old idol, the study of form for itself. For him, as for the anatomists before Darwin, similarity of form is everything and function is of no account.

The special message of Darwin to biology was the vindication of function, and the demonstration that it was the use of parts and not their shape which determined their significance,—that relationship between different types was a question of descent and of survival, and therefore depended not on form but on fitness, that is to say, on physiological function. It is curious to note, with this relapse into scholasticism, the old tendency to intolerance of new ideas and of any light on the problems at issue other than that shed by some enshrined man-made theory at the end of a dark passage. In fact some members of the zoological hierarchy apparently regard the attempt to throw light from any other direction as impious, and associate it, like many worthy divines did the work of Darwin, with the Author of all evil. I would not however like to suggest that Professor MacBride entertained any such comminatory feelings or was conscious of any spirit of religious intolerance when he speaks of the "diabolical ingenuity" of Gaskell's theory. But surely the *odium theologicum* is out of place in dealing with biological problems. A sacerdotal attitude of mind will never advance our knowledge of natural phenomena or of the origin of Vertebrates. It is a happy augury for the revival of freedom of thought in English biology that the Linnean Society should, in this jubilee year of Darwin, have devoted an evening to the discussion of a theory, which, I believe, will prove to be the most important contribution to the history of our race since the publication of the 'Descent of Man.'

Mr. E. S. Goodrich, F.R.S., F.L.S., stated that before embarking on a theory as to the origin of the Vertebrates, we may attempt to determine what must have been the structure of the primitive early Vertebrate from which the Cephalochorda, Cyclostomata, and Gnathostomata (Fish and higher Vertebrates) have been derived. That all these forms are bilaterally symmetrical cœlomate animals, provided with gill-slits, notochord, and dorsal central nervous system, will be granted to start with; but we must further try to find out what has been the general course of differentiation and specialization, to distinguish the higher from the lower forms, and to point out what other characters must have been absent or present from the undifferentiated ancestral stage common to them all.

With considerable certainty Gnathostomes can be traced back to an aquatic fish-like ancestor, in general structure not unlike the modern Selachian. It possessed biting jaws with true teeth, a general covering of denticles, open branchial slits, paired and median fins, a cartilaginous endoskeleton, and well-developed sense-organs.

The Cyclostomes belong to an altogether lower grade of organisation, the primitive characters of which cannot be merely due to degeneration. The segmentation of the body is more complete, and the segments are more uniform. This is especially the case

in the head. The formation of a distinct head-region with a large differentiated brain, a skull, and cranial nerves, is one of the most important and characteristic features of the structure of the Craniata (Cyclostomes and Gnathostomes). It takes place by the gradual modification of more and more of the segments at the anterior region of the body where are situated the mouth, gill-slits, and paired organs of sense. But this process of cephalization has gone much further in the Gnathostomes, where the 9th and 10th cranial nerves become included in the skull, and the corresponding muscle segments are suppressed, than in the Cyclostomes, where these nerves emerge behind the rudimentary skull and the muscle segments still in the adult form an uninterrupted series from in front of the mouth to the tip of the tail. Moreover in the Cyclostomes there are no paired limbs, no true teeth, in fact no trace whatever of dermal skeleton, and the testis has not yet acquired any direct connection with the kidney tubules.

The next point to be studied is the structure of the common ancestor of the Cephalochorda and the Craniata. Now, although *Amphioxus* is doubtless in some respects a very specialized animal—as for instance in the possession of an atrial cavity—yet it preserves many primitive characters. Judging from its structure, we must conclude that the ancestral Vertebrate was still more uniformly segmented than the primitive Craniate. The head-region was scarcely differentiated at all, there was no skull (probably no cartilaginous axial skeleton at all), a quite rudimentary brain, no specialized cranial nerves, no cephalization due to the presence of large paired organs of sense. It is possible that *Amphioxus* is somewhat degenerate; but it cannot seriously be urged that it once possessed in well-developed condition those paired sense-organs which have so profoundly modified the structure of the head-region in the Craniata. For it would be ridiculous to suppose that the modified segments could be restored to their original condition of uniformity with the trunk segments; no trace of the disturbance appearing in either adult or embryo.

Further, in *Amphioxus*, there is no dermal or epidermal armour, and primitiveness is shown in the structure of the endostyle, which becomes modified into the thyroid gland in higher forms. Lastly the presence of true nephridia, a type of excretory organ which has been lost in other Vertebrates, links *Amphioxus* to the lower Invertebrate Cœlomata.

Thus can be traced an irreversible series of stages in the differentiation of Vertebrate structure, at the bottom of which we find a much simpler, but still essentially Vertebrate ancestor, probably already extinct in Silurian times.

Among the various Classes of modern Invertebrates we do not, and indeed cannot expect to find any close allies. But the somewhat distantly related Enteropneusta (*Balanoglossus*) seem to

point to a remote common ancestor in which the supporting notochord was not yet formed, the nervous system was superficial and more diffuse, and the segmentation less perfect.

We have seen that the study of the Vertebrates leads us back step by step to a simple undifferentiated ancestor, in which the complex sense-organs, the highly developed brain, the chambered heart, and other structures so characteristic of this phylum had not yet appeared. Now, the same conclusion is reached on studying such other groups as the Mollusca and Arthropoda. Here also we are led back along an irreversible series of forms to a simpler generalized ancestor. The Vertebrates, Molluscs, and Arthropods, have diverged along fundamentally different lines of differentiation.

Just as the organisation of the Vertebrata is governed by the appearance of a dorsal nervous system, a notochord, gill-slits, a mesoblastic skeleton, etc., so the whole organisation of the Arthropoda is dominated by the secretion of a complete superficial chitinous skeleton, and the accompanying development of jointed appendages serving for feeding and progression. Similarly, the Molluscan organisation has been throughout influenced by the secretion of a calcareous dorsal shell, and the development of a soft body capable of distention by the blood-vascular system. Of all the systems of organs the nervous system may be considered as the most important, and it is just in the study of this system that we can most easily trace the divergence in structure of the three groups.

Owing to adaptation to similar environment or function certain striking resemblances may occur between animals of widely separated origin; this is especially the case with sense-organs adapted to receive definite stimuli. Thus, a Cephalopod Mollusc has a large brain enclosed in a cartilaginous skull, with paired orbits containing large eyes remarkably like those of the Craniate Vertebrate. But the resemblance is due to convergence; these complex organs were not present in more primitive Mollusca, and have been acquired within the Molluscan phylum. Examined carefully they are found to differ as fundamentally in every detail from those of the Vertebrate as does the whole organisation of the Mollusc differ from that of the Vertebrate in general.

Resemblances between the Arthropod and the Vertebrate are not so striking; when they do occur they can be shown to be of the same nature. Here also the various organs which acquire some likeness to each other in the two groups are found to differ as fundamentally in detail as they do in origin. What the two groups really have in common is only that which they have both inherited from a very early undifferentiated ancestral stock.

Dr. H. Gadow, F.R.S. (Visitor), followed, and said:—When Dr. Gaskell explained his hypothesis at a meeting of the Cambridge Philosophical Society, fourteen years ago, I was the only one who had the courage of pleading for its being given a chance. It has survived pitiful contempt and ridicule.

If we want to join the ends of a broken chain, we must be clear about the links. I propose pointing out the last Vertebrate link, by reconstructing an early Vertebrate analytically.

Ever since Gegenbaur based his investigations into the composition of the cranium upon Elasmobranchs, and as since, after him, Balfour discovered so many important features in their embryonic development, the Elasmobranchs have come to be looked upon as the ideally lowest typical Vertebrates. Dohrn even went so far as to explain the Cyclostomes out of the way of direct ancestry as degenerated Elasmobranchs.

This Elasmobranch worship is wrong. They are a side-branch which leads to nothing. The main stem of the Vertebrate descent passes through what we may call Gano-Dipnoi, and their ancestors, Proto-Gano-Dipnoi, presumably were still devoid of paired limbs, and still lower down were not yet Gnathostomes. We can reconstruct further: With a mouth not terminal but ventral: their bulk consisting of a large anterior complex and a short, tapering tail, both segmented and metameric. Condensation and fusion produced a head which was so large because it contained all the principal organic systems, as nervous, digestive, respiratory, vascular, and possibly excretory and generative.

Metamerism in this anterior complex, the incipient head, was doomed, but in the posterior portion it underwent renewed activity. Not only were more segments formed by interstitial budding, but metamerism ran wild, culminating, besides other features, in vertebralization.

The latter proceeded from the tail end forwards, and it is idle to seek for vertebræ in the primitive head, excepting in the part from the vagus backwards, which in the early creature we are dealing with, was a very recent formation.

Meanwhile, the posterior or tail portion becoming larger, part of it, from before backwards, was converted into a trunk, as this was receiving most of those organs which were crowded out from the consolidating head, and also no doubt owing to the repetitional budding backwards of some of these organs. Thus we have arrived at a Tadpole-shaped Vertebrate of which some Ostracodermi with their vertebralized tails are not a bad sample.

Gegenbaur had taught us to consider the spinal cord as an outgrowth from the older brain. The greater part of the chorda is likewise due to a secondary growth backwards, this organ not being laid down in its totality, certainly not in the tail where it ought to have arisen if originally intended for an axial stiffening organ. It arises, however, in the trunk, and since this is a later

addition (due to interstitial postcephalic budding) the chorda must be of a comparatively late stage.

Both these features, chorda and spinal cord, fit into the sketch I have just outlined, but if we consider the spinal cord as an outgrowth from, and therefore a thing later than, the brain, this seems to go strongly against Dr. Gaskell's theory, and this would not be reconcilable with my early Vertebrate. But Gegenbaur's explanation, development from the supra-œsophageal ganglia of the Invertebrates, is one of those captivating notions which is really nothing but a working hypothesis to account for the dorsal position of the spinal cord. And yet this hypothesis, absolutely wrong in detail, led and became wrapped up in the much more important principle of the foundation of a trunk by backward interstitial budding. As this became dimly recognised as reasonable, the spinal cord explanation benefited by it, although wrongly.

A few words about the skeletal material, the cartilage. I remember Gegenbaur saying in his lectures, "Aller Knorpel kommt ursprünglich von Aussen." We are only now beginning fully to understand the meaning of that oracular sentence. The cartilage of the Vertebrata is originally an ectodermal, basal membrane product, which then migrates inwards. It does not arise, as the old master himself had taught, and as everybody teaches, in the immediate vicinity of the chorda, there to form arcualia or basal blocks, these to form neural and ventral processes, whence ultimately arise the median fin-supporting rays. The process is just the reverse. First rays, lastly basal blocks, culminating in the formation of an axial skeleton with centra. As an aside, I need scarcely mention that this reversed process considerably assists the derivation of the paired fins from a hypothetical lateral fin.

Another point: since Gegenbaur has stated it positively, there have been persistent attempts to prove that cartilage appears endogenous in the chorda. Personally I think that this belief rests upon faulty, or misinterpreted observations, but if there should, after all, exist such endogenous chordal cartilage, such an endodermal origin would appear quite irreconcilable with the new doctrine of its ectodermal origin. And yet, if Gaskell's explanation of the chorda as an early folded-off portion of his new gut is right, then it becomes quite comprehensible how this new gut-wall may still retain some lingering scleroblastic cells, since, according to Gaskell, this gut is partly made out of ventral ectoderm.

The early Vertebrate I have just reconstructed approaches the Silurian limbless Ostracoderms. *Pterichthys* may be a belated offshoot, still retaining a pair of Invertebrate limblike appendages. Ostracoderms I hold to be the lowest known Vertebrates, not yet Gnathostomes, whether we call them Hypostomes or Agnatha, or even Cyclostomes in a wider sense.

It is one of Dr. Gaskell's happiest feats to have shown that

Cyclostomes closely resemble such Ostracoderms, not, however, as their descendants, but rather as their ancestors, although modified and even somewhat degenerated. To appreciate this, however, we must cease gazing at the Lamprey. The *Ammocœtes* larva is the key. Of course, even this is not primitive enough for the earliest Vertebrate. To reconstruct this we have to take away its trunk, and such a creature may well be expected to have lived in early Silurian times. Although there is not yet known a single fossil Cyclostome from the Silurian slates to recent river-mud, such creatures may come to light and they would not be more puzzling than *Palæospondylus*.

Thus far it is plain sailing. The Vertebrate end of the broken chain is clear enough. The attempts to bring *Amphioxus* into line have not been successful, and the claims of the other "Chordata" restrict themselves to a few features of doubtful value. Nowhere could these comparisons be driven home, and what do these attempts amount to against Dr. Gaskell's detailed, almost too minute comparisons of a dozen of the most important organs? If his results were, every one, nothing but coincidences, analogies, such a state of things would be much more astonishing and unlikely than his whole hypothesis. His explanations of the huge cavities in the brain, the peculiar structure of its roof, the ventral and the neurenteric canal, are the only plausible ones ever offered. It is a somewhat forgotten fact that in some Birds there is no proper neurenteric canal, while in other species there are, not one, but two and even three successively formed communications of the central canal with the gut and passing right through the chorda. An organ which, like the chorda of a bird, has passed its prime, is liable in its degeneration to revert to primitive features, somewhat muddled. Here we have three neurenteric connections, their respective funnels behaving as if the chorda were a negligible quantity, or rather part of the gut.

Gaskell's explanation of the chorda is by far the best we have. If considered as a product of an endodermal gut, the chorda cannot well have started as a supporting organ. It must have started with gut-like function, but having lost this with its lumen, its walls shrinking to rod-shape, may then well have formed a useful axial support. Can it be upheld, that the chordoids of *Balanoglossus* and *Rhabdopleura* ever had a gut function? This would mean that a glandular, secretive organ has lost its function and yet waxed large. A proper chorda is not a glandular thing, and even when it is a rod ten feet long and more than one inch thick, it possesses neither nerves nor blood-vessels.

Zoologists have allowed histology to slip out of their hands into those of the physiologists, and it has done well there. Embryology would likewise have fared better if the function of the aggregating and growing masses of cells had been taken as the leading principle, instead of the structures which they ultimately give rise to. It is function which determines the organ, and the

possible function often depends upon mere position, sometimes almost accidental, with regard to the surrounding medium. Nature does not care where the material comes from, provided it be suitable. There are, for instance, endodermal and ectodermal gills; nor does it matter whether a creature digests and absorbs food by its inner or by its outer surface. Whilst an armour-clad animal cannot do it, a naked Amphibian drinks through its whole skin; and most species of *Spelerpes*, sometimes six and more inches long, never possess gills, have lost their lungs, and breathe almost entirely through their outer surface.

The Germ-layer theory has crystallized into a dogma and has led into a *cul-de-sac*. How else could it happen that people, who have spent a lifetime at embryology, throw it up in disappointment and denounce the theory of Recapitulation, which is about the only valuable, really priceless generalization of this direct means of studying evolution.

Because Dr. Gaskell is a good physiologist, he saw that the central canal and the brain ventricles could not possibly have anything to do, primarily, with the central nervous system, that, in fact, they are the remnants of a gut. This has of course been suggested long ago, from the general look of the thing, but there were no proofs, and there was the seemingly hopeless task of having to account for a new gut. Gaskell had the courage and insight to show how such a gut may have been evolved, and this is one of the best, simplest and most convincing chapters. It is a false dogma that the gut must be *the* organ which is homologous in all gut-possessing animals.

Dr. Gaskell may be mistaken in some of his interpretations, but his hypothesis is not only at least as good as others, but it is the only one which endeavours to carry through a great number of comparisons. His hypothesis is logically conceived; it is built up of items, none of which are impossible, therefore the total is possible.

The discussion was then adjourned to the next General Meeting, Thursday, 3rd February, 1910, at 8.0 P.M.

February 3rd, 1910.

Dr. D. H. Scott, M.A., F.R.S., President, in the Chair.

The discussion upon the Origin of the Vertebrates, begun at the previous Meeting, was resumed.

Dr. A. Smith Woodward, F.R.S., F.L.S., remarked that Palæontology affords no clue to the ancestry of the Vertebrates, because they seem to have originated as animals with no hard parts capable of fossilization. When they first acquired a calcified skeleton in the Upper Silurian period, they were represented not only by very primitive types like the Ostracoderms, but by true fishes of at least as high a grade as the Elasmobranchs (Acanthodians).

It is perhaps a significant fact that the Arthropods were the dominant type of life at the time when the Vertebrates began to be conspicuous. It is known that during the subsequent course of evolution of the Vertebrates themselves, each successively higher great group became the dominant type for the time being; and that each advance was due to evolution from the immediately preceding dominant type. In every case, however, the higher group seems to have been directly derived from the earliest and most generalized members of the preceding group, not from the specialized members that flourished at the time of its dominance. If, therefore, the Vertebrates originated from Arthropods, their direct ancestors must have been early generalized forms which there is little hope of discovering among fossils.

Although so little is known of their organisation, it seems probable that the Ostracoderms are lower in rank than the true fishes, and most nearly related, among surviving animals, to the Marsipobranchs. Dr. Gaskell has added to this probability by his researches on the Ammocœte. His comparison of the structure of the dermal head-shield in the Upper Silurian *Auchenaspis* with that of the more deeply seated plate of muco-cartilage in the Ammocœte, is particularly striking and interesting.

Most of the Ostracoderms have a remarkable superficial resemblance to the contemporaneous Arthropods of the Eurypterid group, being adapted for a similar mode of life on the sea-bottom. A few, however, are laterally compressed and as gracefully fusiform as swiftly-swimming fishes (e. g., *Birkenia*); and that these had a wide geographical distribution in Upper Silurian times is shown by the recent discovery of a fragment (named *Ctenopleuron nerepisense* by G. F. Matthew) in New Brunswick.

The supposed discoveries in Ostracoderms of appendages comparable with those of Arthropods, are due entirely to faulty observation or misinterpretation. There is nothing more than a normal branchial chamber on each side of the cranial region in genera such as *Cephalaspis*, *Pteraspis*, *Cyathaspis*, and *Trematuspis*, where the skeleton can be well observed. The so-called paired appendages ascribed to the trunk of *Cephalaspis* by Prof. W. Patten, are merely the scales which project along its sharp angulation on each side.

Prof. Arthur Dendy, F.R.S., Sec.L.S., contributed the following remarks :—

Any theory of the origin of Vertebrates must stand or fall by the results of detailed criticism of the evidence upon which it rests, and owing to the large amount of evidence which Dr. Gaskell has brought forward, this must necessarily be a very laborious undertaking. The portion of this evidence to which I wish to call special attention on this occasion is that which concerns the eyes, upon which very great stress has been laid. This applies especially to the median eyes, concerning which Dr. Gaskell himself states* that "undoubtedly, in recent times, the most important clue to the ancestry of Vertebrates has been given by the discovery that the so-called pineal gland in the Vertebrate brain is all that remains of a pair of median or pineal eyes, the existence of which is manifest in the earliest Vertebrates." This being so, it seems especially desirable to examine critically the evidence brought forward in this case. Dr. Gaskell has studied these organs in the Ammocœte larva of *Petromyzon*. I myself have studied them in the *Velasia* stage of the New Zealand Lamprey, *Geotria*, which is very closely related to *Petromyzon*, and also in *Sphenodon*, where they are exceptionally well developed. I may say at once that my interpretation of their structure does not agree with that of Dr. Gaskell.

Dr. Gaskell reminds us that Crustaceans and Arachnids, as well as Vertebrates, have lateral and median eyes and that in these Arthropods, "the median eyes are in all cases eyes with a simple upright retina and a simple cuticular lens, while the retina of the lateral eyes is compound or may be inverted, according as the animal in question possesses crustacean or arachnid affinities." Again he says, "The lateral eye of the vertebrate, possessing, as it does, an inverted compound retina, indicates that the vertebrate arose from a stock which was neither arachnid nor crustacean, but gave rise to both groups—in fact, was a member of the great palæostracan group." He then proceeds to examine the evidence with regard to the median eyes of *Ammocœtes*, with a view to discovering whether they belong to the same type as those of Arachnids and Crustacea. He compares an extremely diagrammatic figure of the pineal eye of *Ammocœtes*, which in my opinion is far from being correct, with an apparently equally diagrammatic figure of an *Acilius* larva, which, to judge from the drawing of this eye copied from Patten on a later page, is also far from accurate. By this procrustean method of treatment the two eyes are certainly made to look very like one another, although it has been impossible to eliminate the cuticular lens of *Acilius*, which is entirely wanting in *Ammocœtes*.

The manner in which it has been necessary to treat the evidence in order to arrive at this comparison is clearly illustrated by

* 'The Origin of Vertebrates': Longmans, Green, & Co., 1908, p. 74.

Dr. Gaskell's discussion of the minute structure of the retina. If the comparison is to be valid the retina of the pineal eye must be a simple retina, that is to say, it must not contain an optic ganglion. Dr. Gaskell says "neither I myself nor Studnicka have been able to see any definite groups of cells between the nerve end-cells and the optic nerve such as a compound retina necessitates." It is difficult to reconcile this statement with what Studnička himself says. According to this author,* the retina of a developed Ammocœte consists of the following cell-layers:—

(1) At the bottom, a layer of nerve-fibres, which are in direct connection with those of the pineal nerve.
(2) A layer of basal cells; large, very clear cells with lightly staining protoplasm and large nuclei, with a number of nerve-fibres running between them.
(3) A layer of nuclei belonging to small cells.
(4) A layer of cylindrical cells which correspond to the rods of older authors and which consist of sense-cells and supporting cells.

This does not sound very much like a simple retina. Dr. Gaskell quotes Studnička as saying that the nerve end-cells pass directly into the nerve, which, Dr. Gaskell observes, "points directly to the conclusion that this retina is a simple, not a compound retina, and that it therefore in this respect agrees with the retina of all median eyes." I do not know where Studnička makes the statement upon which Dr. Gaskell bases this conclusion. What I do find him saying (*op. cit.* p. 25) is that the lower extremity of the sense-cell is produced into a nerve-fibre which loses itself in the nerve-fibre layer of the retina (1). He further expressly states that in the adult *Petromyzon* there are amongst the round basal cells many which undoubtedly have the character of ganglion cells, and that the processes of these cells may be followed into the layer of nerve-fibres, while they also send processes into the layer of cylindrical cells.

In short the retina of the pineal eye of *Ammocœtes* is undoubtedly a compound retina and not, as Dr. Gaskell would have it, a simple one. My own observations on the pineal eye of *Geotria* fully confirm this view. In this animal also a well-developed retinal ganglion is present. Dr. Gaskell endeavours to harmonize my observations with his theory by supposing that the cells of which this retinal ganglion is composed "do not represent the original optic ganglion of a compound retina, but rather the subsequent invasion, by way of the pineal nerve, of ganglion cells belonging to a portion of the brain." When undoubted facts have to be ignored or explained away in this manner in order to

* "Die Parietalorgane" (in Oppel's 'Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbelthiere'), p. 24.

support a theory it looks as if that theory must stand upon a somewhat shaky foundation.

Dr. Gaskell, then, concludes that in the pineal eye of *Ammocœtes* "there is certainly no appearance in the least resembling a compound retina such as is seen in the vertebrate or crustacean lateral eye." It is true that in the Lampreys the retinal ganglion of the pineal eye is not spread out to form a layer of such uniform thickness as in the lateral eye, but the pineal eyes of *Sphenodon* and of the Lacertilia make a much closer approach to the lateral eyes in this respect.

By far the most important evidence afforded by both the pineal and lateral eyes of Vertebrates, however, is, in my opinion, that derived from their development. Both differ essentially from any Invertebrate eye in being formed as diverticula of a hollow brain. The eyes of Arthropods are formed by thickening and differentiation of the superficial epiblast. How is it possible to reconcile this discrepancy? Dr. Gaskell himself (*op. cit.* p. 101) states the problem quite clearly in the case of the lateral eyes. Having arrived at the conclusion that the retina is in this case a compound retina, composed of a retina and retinal ganglion of the type found in Arthropods, he goes on to say: "From this it follows that the development of the vertebrate retina ought to show the formation of (1) an optic plate formed from the peripheral epidermis and not from the brain; (2) a part of the brain closely attached to this optic plate forming the retinal ganglion, which remains at the surface when the rest of the optic ganglion withdraws; (3) an optic nerve formed in consequence of this withdrawal, as the connection between the retinal and cerebral parts of the optic ganglion." Of course, the same must apply to the pineal eyes *.

Relying upon Götte's observation "that the retina arises from an optic plate, being the optical portion of his 'Sinnesplatte,'" Gaskell concludes that the retina (of the lateral eye) is to be regarded as a portion of the superficial epiblast together with a retinal ganglion with which it has become fused, while the optic vesicles are explained as outgrowths of the primitive Arthropod stomach which supply only the epithelial and supporting framework of the retina, with which the nervous and sensory elements become interwoven. The development of the lateral Vertebrate eye is, however, a very complex process, and as I have not made a special study of it myself, I leave it on one side, though I may say that Dr. Gaskell's idea of the double origin of the retina and its supporting structures seems to me to be too far-fetched to be of much value as a support for his theory, and that any attempt to institute a close comparison between the lateral eye of a Vertebrate and the highly specialized compound eye of an Arthropod is foredoomed to failure.

* At any rate so far as no. (1) is concerned, whatever view we may take as to the presence or absence of a retinal ganglion in the pineal eye.

Dr. Gaskell unfortunately does not deal with the development of the pineal eye, which is far simpler. This has been carefully studied is various types, all of which agree in essential features. I myself have studied it chiefly in *Sphenodon*, upon which animal the following statements are based. The pineal eye originates as a simple evagination of the brain-roof. This completely separates from the brain and closes up. The optic vesicle thus formed does not invaginate to form an optic cup, as in the case of the paired eye, but the retina, with its sense-cells, ganglion-cells and nerve-fibres, is formed directly and *in situ* by differentiation of its posterior wall, while the lens is formed from its anterior wall. There is not the slightest indication of the origin of any part of the retina directly from the superficial epiblast. It is true, of course, that the whole of the central nervous system is derived, in the first instance, from superficial epiblast, and so also is the central nervous system of an Arthropod. No one denies that the retina is epiblastic in orgin; the question is, what part of the epiblast is it derived from? In the Vertebrate it is derived from the part which becomes invaginated to form the central nervous system. In the Arthropod and in other Invertebrates, it is not.

I cannot, therefore, avoid expressing the opinion that the evidence which Dr. Gaskell derives from the study of the lateral and pineal eyes in favour of his theory does not stand the test of critical examination. It appears to me, if I may venture to say so, that he has failed to distinguish between analogy and homology. Animals which have to live under similar conditions must be expected to become adapted along similar lines, and it is no more necessary to invoke a common ancestry to explain the resemblance between the visual organs of Vertebrates and Arthropods than it is to give the same explanation of the superficial resemblance between their organs of locomotion. Again, the resemblance between the lateral eyes of Vertebrates and the highly characteristic compound eyes of any Arthropod is not nearly so striking as is that between the former and the higher Cephalopod eye, and yet no one, so far as I am aware, has yet ventured to include the Octopus in the ancestral portrait gallery of the Vertebrata.

Looking at the problem for a moment from a wider point of view, I should like to express my agreement with those who see in *Amphioxus* a close approximation to the starting-point of the great Vertebrate phylum. The evidence in favour of the essentially primitive character of *Amphioxus* is, to my mind, overwhelming, but the acceptance of this evidence is fatal to Dr. Gaskell's views, for in *Amphioxus*, of course, a very large proportion of the Vertebrate characters upon which he lays so much stress as indicating Arthropod affinities, have not yet put in an appearance. Thus, for example, there is no trace of either lateral or pineal eyes, and we therefore conclude with confidence that

these structures have not been inherited from any Invertebrate ancestor at all, but have arisen quite independently within the Vertebrate group.

In connection with Dr. Gaskell's theory, the question is sometimes asked:—If the cavity of the central nervous system of the Vertebrate, with its lining epithelium, has not been derived from the alimentary canal of an Arthropod ancestor, how do you account for its existence, and how do you account for the existence of the choroid plexuses? To the zoologist, of course, this question presents no difficulty. One of the commonest phenomena of development throughout the Animal Kingdom is the increase of surface by the formation of folds. We are familiar with it in glandular tissues and in respiratory tissues, and we are familiar with it also in the formation of the central nervous system of various Invertebrates, as Professor MacBride has already pointed out. No one doubts, moreover, that this is the explanation of the convolutions of the brain in higher Vertebrates. Why then object to apply the same principle in explanation of the origin of the Vertebrate nervous system by invagination of the superficial epiblast? The Vertebrates inherited from their Invertebrate, worm-like ancestors, this characteristic mode of forming the central nervous system, which naturally resulted in the development of a hollow tube with at first a narrow lumen. Further evolution of the nervous system was brought about primarily by the increase in number of the nerve-cells and the consequent thickening of the wall of the neural tube. It will, of course, be asked by the supporters of Dr. Gaskell's theory, why has the cavity of the original neural tube increased to such enormous dimensions in the case of the ventricles of the brain? Here again I do not see any difficulty. The great mass of nerve tissue formed in the brain requires some very well developed system for nutrition and respiration. This is primarily effected of course by the cerebral blood-vessels; but we have also the cerebro-spinal fluid, with which the ventricles of the brain and the *canalis centralis* of the spinal cord are filled, and which probably exercises an important respiratory and possibly also other functions. I suppose Dr. Gaskell will hardly ask us to look upon the cerebro-spinal fluid as representing the digestive juices which were poured into the stomach of the ancestral Arthropod.

What about the choroid plexuses, then? Here, again, we have a beautiful illustration of the principle of folding in order to increase surface, a folding which is quite inexplicable except on the assumption that the choroid plexuses fulfil some very important function in connection with the cerebro-spinal fluid into which they dip. They are, as everyone knows, extraordinarily vascular (which the wall of the Arthropod stomach is not), and they probably constitute a kind of intra-cerebral gills concerned in the respiration of the cerebro-spinal fluid; they may also have other functions in connection with this important fluid.

It appears from Dr. Gaskell's opening speech that he assumes that the anterior opening of the neural tube in the larval *Amphioxus* represents the old Arthropod mouth, but in the higher Vertebrates he locates this ancestral mouth in the region of the infundibulum. This necessitates the supposition that the anterior neuropore is identical in position with the infundibulum, a supposition which would, I imagine, strike modern embryologists with amazement.

Then again, what is the value of the evidence afforded by the so-called neurenteric canal? This structure, if structure it can be called, simply results from the fortuitous enclosure of the blastopore by the uprising neural folds, and to my mind it has no phylogenetic significance of the kind attributed to it by Dr. Gaskell.

It was urged, I think by Professor Starling, that the immense physiological importance of the central nervous system gives it a special claim to consideration as evidence in the discussion of the origin of Vertebrates. This is entirely contrary to the usually accepted views of systematic zoologists, who find in structures which are apparently of the least use to their possessors * the best guides to genetic affinity. Organs which are of great use must be subject to adaptive modification in accordance with the changing needs of the organism. Modern schemes of classification are indeed largely based upon this principle, and certain modifications in the nervous system of tape-worms have been explicitly ruled out as guides to classification in accordance therewith.

[The central nervous system of a Vertebrate of course agrees with that of an Arthropod in exhibiting traces of a fundamental metamerism, because both Vertebrates and Arthropods are metamerically segmented animals, and both have very probably been derived from some metamerically segmented common ancestor.

It is the later modifications, cœnogenetic rather than palingenetic features, readily explicable as adaptations to the special needs of the Vertebrate organisation (which are of course in many respects similar to those of the Arthropod organisation), that I consider to be inadmissible as evidence in considering the phylogenetic relationships of the Vertebrates. The fact that highly specialized characters of the brain may afford a useful clue to relationship *within the limits of the Vertebrate phylum* does not, in my opinion, affect the question at issue. In dealing with closely related groups comparatively recent modifications are of undoubted taxonomic value; but in comparing such widely divergent groups as Vertebrates and Arthropods, resemblances due to such characters, when they can be explained quite reasonably as the result of convergent evolution, must be eliminated from the discussion.]

* I may cite in illustration the microscleres or so-called flesh-spicules of siliceous sponges, with their extraordinarily diverse and apparently specifically constant modifications.

Sir Ray Lankester, F.R.S., F.L.S., said he was not prepared there and then to discuss points of detail, but the subject was so interesting that he should wish to offer some remarks. Moreover he gathered from Dr. Gaskell's book, and from more direct information, that he himself was to some extent connected with the genesis of Dr. Gaskell's views, since certain observations and arguments of his own on *Limulus* and the Scorpion had germinated in Dr. Gaskell's mind and led him to the very careful and elaborate studies which he had made and the extraordinary theory which he advanced. Whilst calling it an "extraordinary" theory, he did not wish it to be supposed that on that account he wished to reject it or not to give it full attention. This was a matter not to be treated as *à priori* impossible or improbable, but the question simply was, "Are the facts brought forward by Dr. Gaskell such as to make it appear probable that the Vertebrates have developed from Arthropods resembling *Limulus* by the conversion of the old alimentary canal into the neural tube and the simultaneous formation of a totally new digestive tract?'

The relations of animal forms to one another is the great problem of morphology. A hundred and twenty years ago morphologists still believed in the "scala naturæ" and a linear progressive series of animal groups. The great step was taken by Cuvier in opposition to the conception of Lamarck of arranging animal forms in four branches—"embranchemens" he termed them, the Radiata, Mollusca, Articulata, and Vertebrata. He thereby anticipated the modern conception of a branching pedigree, which became the generally accepted form of classification when once Darwin had established the theory of Descent.

The earlier attempts at a branching pedigree made by Haeckel differed from the later ones by the same naturalist, and there had been considerable development and improvement in the theoretical pedigree, which aimed at exhibiting the genetic affinities of all animal forms. The question of the position of the Tunicata had been one of the most interesting. Allman, forty or more years ago, considered the Tunicata as related together with the Polyzoa to the Lamellibranchs and other Mollusca. He regarded the perforated pharynx of the Ascidian as formed by the fusion of the gill-plates of a Lamellibranch along their free edges to form a closed sac, and this was perhaps the largest call upon the imagination which had been made by a modern morphologist until Dr. Gaskell suggested the conversion of the Arthropod's digestive tract into the spinal cord and the formation of a new gut in Vertebrata by the closing in of an open ventral groove. The facts brought forward by Kowalewsky had determined the position of Ascidians in the Vertebrate stem. There were four "coincidences" of structure which by the law of probability led to the conclusion that Ascidians were genetically closely related to Vertebrata. They were the existence in the Ascidian tadpole as well as in Vertebrata (1) of the notochord developed from endoderm,

(2) of the pharyngeal gill-slits, (3) of the tubular dorsally placed nerve-cord, and (4) of the cerebral eye. The evidence was cumulative, and its value depended on the exact and indisputable nature of the agreements and on the fact that they were found in the two cases compared and in no other animals, so that a common inheritance of these structures by Ascidians and certain Vertebrata, not shared by other forms, was the only rational explanation of the facts. Was this the case with the coincidences of structure between the Lamprey and the Arthropods brought forward by Dr. Gaskell? Sir Ray Lankester held that the coincidences cited by Dr. Gaskell were not of a sufficiently exact and special nature, nor peculiar to the Vertebrates and Arthropods, so as to render it necessary to suppose that Vertebrates had been derived from Arthropods, and certainly not of such a nature as to render it reasonable to suppose that the extraordinary conversion of the Arthropod's digestive tract into the nerve-tube had taken place as insisted upon by Dr. Gaskell.

The view which was almost universally accepted at present by zoologists was that when once we pass from the Cœlenterate or Entero-cœlous grade of animal structure to the Cœlomata or Cœlomo-cœlous grade, a number of diverging great lines of descent or phyla must be recognised—such as the Echinoderma, the Appendiculata (including Arthropods, Rotifers, and Annelids), the Mollusca, the Vertebrata, the Nemertina, and other worm-phyla. As to the beginnings of any of these lines of descent, we had (as was natural enough) very scant indications, nor could we say anything as to the early connection of any one of these great phyla with another. What appeared highly probable, if not certain, was that they all converged to simpler ancestral forms, and that they all inherited the same fundamental tissues, digestive tract and glands, nephridia, cœlom and cœlomic ducts, reproductive gonads, blood-vascular system, and nervous cords (many or few), and essentially the same types of sense-organs—ophthalmic, auditory, gustatory, olfactive, and tactile. That the optic vesicles of Arthropoda should agree, not absolutely but in many important respects, with those of Vertebrata, could not be held to indicate special affinities since Annelids, Molluscs, and even Echinoderms had organs of the same kind. That some of the tissues should agree minutely in two of the phyla was not suggestive of special affinity, since many of the tissues agreed in most of the larger phyla. Sir Ray Lankester held and he desired to state it without any offence, that in searching by long and strenuous enquiry for evidence in favour of such a hypothesis as that adopted by Dr. Gaskell, the mind is liable to a kind of "suggestion," and that the psychological condition may become similar to that of those who too readily admit all sorts of coincidences as evidence that Bacon wrote the plays of Shakespeare. The heroic nature of the task which it is sought to accomplish undoubtedly in many enterprising and devoted investigators has re-acted unfavourably on the

judgment. All are liable to it and it may be that something of the kind is here at work. Though he could not follow Dr. Gaskell in the theory put forward by him as to the origin of Vertebrates, he recognised very gratefully the value of the observations on many details of structure to which it had led that distinguished physiologist, and also the new observations which it had called forth on the part of other naturalists, such as the interesting additions to our knowledge of the head-shield and the body-scales of *Cephalaspis* which had just been placed before the meeting by Dr. Smith Woodward. He thought the Society was to be congratulated on a very interesting debate. (In the further course of the discussion Sir Ray Lankester stated that whilst he considered *Amphioxus* and the Ascidian tadpole to present in many points of structure a very much more primitive phase of the Vertebrate group than do either Lampreys or Fishes, he held that they were also specially modified and degenerate each in its own way, and were not closely representative of the main line of descent. He considered that the remains of the earliest known fossil fishes, on account of their necessarily incomplete condition, were not capable of throwing much light on the question of Vertebrate ancestry. He was led to the conclusion that *Balanoglossus* threw some light on the subject, and he drew attention to the remarkably complex brain and cerebral respiratory pits of the Nemertine worms and the dorsal median as well as lateral nerve-cords of those creatures, which had led Hubrecht long ago to suggest their close connection with the remote ancestors of Vertebrates. A large survey of the facts of animal structure, even including that of unfamiliar marine worms, was necessary in order to form a reasonable judgment on the question of Vertebrate ancestry.)

Dr. P. Chalmers Mitchell, F.R.S., F.L.S., remarked that consideration of the general morphology of the nervous system enables us to place the Vertebrates in their true perspective amongst the various Invertebrate groups. In the Cœlentera, as shown by the Hertwigs, the nervous system frequently appears as a diffuse layer of cells and fibres underlying, and in close connection with, the epidermis, whilst there is much evidence that a similar primitive condition underlies the various presentations of the nervous system in higher groups. Even amongst the Cœlentera, two processes coincidently or independently result in modification of the primitive simplicity. The original diffuse layer may become thickened in definite regions, forming, for instance, rings round apertures or radial bands, whilst in the intervening areas it may be obliterated. The thickened bands or rings may migrate inwards and lose their intimate connection with the epidermis. Similar processes varying in position and extent of their incidence have led to many different arrangements of the nervous system in the higher groups.

In the Turbellaria, inward migration has taken place, and two ventro-lateral cords have been formed.

In the Trematodes, inward migration has taken place, and there are six cords, two dorsal, two ventral, and two lateral, with a network of connecting cords, some of which form a series of hoop-like rings.

In the Cestodes there is less inward migration, whilst there are two lateral cords with occasional transverse connections.

In the Nemertines, sometimes there is no inward migration, so that the nerve-strands remain strictly sub-epidermal; sometimes the strands have completely separated. The primitive continuous sheath is frequently retained with two lateral and sometimes one dorsal thickening.

In the Nematodes also the extent to which inward migration has taken place varies very much, in some cases the sub-epidermal position being retained. Six strands occur in many forms, one dorsal, one ventral, and two at each side; these are connected by traces of the primitive continuous sheath in the form of a very broad anterior hoop, and narrow posterior strands. A different arrangement of these antero-posterior strands occurs in front of the nerve-collar.

In *Gordius*, inward migration has occurred and there are three ventral strands.

In Arthropods, the inward migration and separation from the epidermis are complete, and there are two ventral bands with an anteriorly placed collar.

In *Balanoglossus*, there is a continuous sub-epidermal sheath which has not migrated inwards, and special dorsal and ventral thickenings, and also in the collar region the very interesting short neural tube with anterior and posterior neuropore formed by invagination.

In Chordates, there is a single dorsal band which migrates inwards, whilst the outgrowing segmental nerves may be taken as specialized representatives of the continuous sheath.

From the point of view of the general morphology of the nervous system, therefore, the Chordate or Vertebrate group exhibits simply one of a large series of different modes of specialization of the primitive diffuse, sub-epidermal sheath.

In quite a number of these different experiments, the processes of segmentation and of cephalization with the formation of a brain have occurred independently, and have produced analogical or homoplastic structures. The elaborate comparison of the results of the processes of cephalization and segmentation in *Ammocœtes* and higher Vertebrates with those of the Arthropods are meaningless unless we suppose that *Amphioxus* has passed through such a stage and has lost all traces of it; it is a simpler supposition that the higher Vertebrates have independently acquired the results of cephalization after having passed through a stage of which *Amphioxus* is the nearest living although specialized and degenerate representative.

As Prof. Gaskell has laid so much stress on comparison between

the brain and central nervous system of Arthropods and Vertebrates, it is interesting to notice that C. Judson Herrick, another distinguished physiologist and psychologist, has recently compared the two sets of organs (Address of the Chairman of the Section Zoology; American Association for the Advancement of Science, 1909, printed in 'Science,' 1910, p. 7). Professor Herrick, reviewing the subject without reference to any theory of origin, comes to the conclusions that the psychological processes of Arthropods and Vertebrates differ totally; that the difference of function is correlated with a fundamental difference of type underlying all superficial resemblances, and which was "foreshadowed far back among the ancestral crawling things in which no truly vertebrate character was manifest, foreshadowed merely by a structural type with different latent potencies."

Professor Stanley Gardiner, F.R.S., F.L.S., said:—Of the many speakers only Dr. Gaskell has put forward a connected theory which the rest have merely attempted to destroy. Their alternative plan is by a line of evolution through *Amphioxus*, but they do not attempt to show us how this beast may have been produced. Unfortunately in the whole question of the Origin of Vertebrates we have very few real facts upon which to base our views. Such facts, so far as I can see, will be obtained from the study of extinct forms, and it is a most curious fact that nowhere has Palæontology yet shown a series of transitional types between distant groups. We have to content ourselves with *conclusions from analogies* and *proofs by probabilities*. We largely study existing forms. The danger of this is well exemplified when we consider the relations of Reptiles to Mammals. Both groups as existing now must largely be traced to *Theromorphs*, of which, following Cope, minute and relatively puny forms probably branched off into each of the two phyla. Applying the ordinary terminology of Cope, it may be said that existing Reptiles have regressed and that existing Mammals have progressed. We may now consider this line as fairly well established by *analogies* and *probabilities*, and it appears to me that it is a line almost of facts to which we can appeal with considerable certainty for zoological canons. If there is one point more than another which it shows it is surely the paramount importance of considering the condition of the central nervous system a test of progression, as Dr. Gaskell maintains. It demonstrates with certainty that his deductions from the brains of living Vertebrates, as such a test, are absolutely justified. In opposition to Professor Dendy I should claim that the central nervous system is the best organ on which to trace the changes of evolution. It governs every organ in the body, and it must reflect in its own structure every change which those organs undergo, every act of progression.

Turning to Amphibia, we have no indications of their real origin, and we have still less when we come to the Fishes. The

Leptocardia and the Marsipobranchia are with no certainty represented in the fossil state. They are derived from an ancestor far more ancient than the *Theromorphs*, and any comparison of existing forms, supposed to have been derived from this ancestor, might well show vastly greater differences than between say Primates and Lacertilia, or even Primates and Pisces.

The weakest part of the MacBride-Goodrich argument the other night lies in their consideration of *Amphioxus* as a simple primitive Vertebrate. Whatever *Amphioxus* may be, it is surely not in the main stem of the Vertebrate descent, and it is certainly a very specialized form. To argue, as Goodrich did, that the presence of primitive excretory cells (solenocytes) in *Amphioxus* proves it to be primitive, and related to the Annelids, comes to the same thing as claiming that *Phoronis* is also an Annelid, because its larva has similar cells.

Examining both the above groups, and applying "every canon of Biology," we must, I conceive, regard *Amphioxus* as equally typical of regression as is any beast that exists in the Animal Kingdom, while the Marsipobranchia as typically show progression. Looking at the groups from this point of view the Leptocardia may be cast aside from our discussion as unprofitable, and we can turn with certainty to considering the morphology of Marsipobranchs for some guide to the evolution of Vertebrates.

It is not my desire to draw your attention to the series of facts, both physiological and morphological, discovered by Dr. Gaskell in his extensive comparison of the higher Invertebrates with the lower Vertebrates. They present an extraordinary series of analogies and probabilities which cannot be lightly passed over, and, even if his views be ultimately rejected by palæontological discoveries, will for ever make Zoologists indebted to him for drawing their attention to a fresh and broader aspect in which to consider their science. Of his comparisons I would particularly draw attention to that between the internal cartilaginous skeleton of *Limulus* and that of *Ammocœtes*, the skeleton being a part which, judging from fossil and living Vertebrates, seems to retain for the longest period traces of all its developments, "earmarks," as Osborne terms them. I might refer also to the infundibulum, the commissures of the brain, the thyroid, the auditory apparatus, and the existence of giant fibres and cells in the nervous system. By far the simplest way to explain this extraordinary series of coincidences between the organs of different forms is to suppose that they are due to a common inheritance.

I would turn now rather to the difficulties which beset the view, and by far the chief of these must be deemed to be that relating to the alimentary canal. To get that of *Petromyzon* from that of *Ammocœtes* we have an entirely new formation of quite startling character. This is a fact, and accepting it as such we can proceed with our minds more open, I think, to consider how a gut in Vertebrates came into existence. Professor MacBride is quite

Haeckelian in his views of the gastrula—or at least of the germ-layer theory, which he claims to be stronger than ever. If there is a real fundamentally important separation such as he claims between the germ layers, it is quite inconceivable that there could be formed cells of one layer from those of another layer. In regeneration of tissues we have clear evidence that ectoderm can form mesoderm and endoderm, that endoderm can form ectoderm and mesoderm. Mesoderm is not very happy in its formation of the other layers, but Dendy has shown that in *Antedon* the endoderm can come from ectoderm and from mesoderm.

I would altogether dissent from Sir Ray Lankester's line of evolution from the gastrula. I am inclined myself at present to regard the Annelids as coming from some Actinian-like ancestor. In this, as in all Actinia, the secreting digestive epithelium, that of the stomodæum and mesenterial filaments, is derived from (grows down from) the ectoderm after the whole of the gastro-vascular cavity is lined by an epithelium which is capable of ingestion but not of extracellular digestion. My own work is not sufficiently advanced perhaps for me to make this statement, but such were the indications I obtained. The lining epithelium of the cavity would be equivalent to and homologous with the endoderm of *Hydra*, and it would form the mesoderm of three-layered animals, the endoderm being an entirely new formation. I am aware that there are great, even insurmountable, difficulties in respect to this view, but the ectoderm and eudoderm of higher forms appear to me to be far more intimately related in their functions than are either of them to the mesoderm.

In the experimental work of Driesch, Wilson, and others, we get into a maze of difficulties in regard to the preformationist hypothesis. Blastomeres, it is clear, are to a large degree interchangeable. Incidentally, a fourth blastomere gives a gastrula in *Amphioxus*. Again, in budding there are difficulties with this theory, the gut of some budded-off Polyzoa being formed from mesoderm, while of Tunicates, supposed relations of the Vertebrates, *Clavellina* buds from the endoderm and *Botryllus* from the ectoderm, giving ectoderm and endoderm respectively; and do not some Sponges turn inside out to give the adult?

I need scarcely go further into the question of the germ-layer theory. The confusion when it is applied to Vertebrates is obvious, and we get everywhere involved in difficulties in Invertebrates. If the gastrula be a general stage on which great stress is to be laid, it necessarily might be supposed that the stages up to it should be the same, while actually in the segmenting eggs we get the most diverse fates for the individual cells.

On the whole it is abundantly clear, it appears to me, that it is the nurture as well as the nature of the individual organs which is to be discussed. The law of recapitulation in embryology has only a limited applicability. Surely the transitory characters are at best only a very partial reminiscence of the structural types

through which the adult may be supposed to have passed during the geological ages. In all these stages the embryo has itself been subject to specialisation. I think that where Dr. Gaskell errs is in laying too much stress on many details of the recapitulation hypothesis. Some of his resemblances I can conceive might be due to convergent or adaptive evolution, acting upon lines almost infinitely long before the common ancestor is reached. Yet there remains such a mass of hard analogy, borne out too by the most careful physiological and morphological investigation, a mass which cannot be put forward—or even a tithe of it put forward—by the exponents of any other view, that one is inclined to doubt the presence of adaptive evolution at all in this case. Although I should feel it to be "non-proven," I cannot but regard it as by far the most striking view of the origin of Vertebrates that has yet been expounded.

Morphologists must carefully consider whether they may not be holding on to shibboleths, and wilfully blinding their eyes to the great mass of facts, many largely physiological, which has in recent years been accumulated. Is it not just as necessary for the zoologist, who wishes to consider these great questions, to be a physiologist as it is for the latter to be a morphologist? If it is desired to prove Dr. Gaskell's hypothesis wrong, his points must be taken fact by fact to see where they lead—as indeed barristers do with evidence in our courts. If it is desired to prove some other theory right, it must likewise be taken fact by fact, and no one can, as some try to do at present, consider the nature of any beast without any examination into its nurture.

The Rev. T. R. R. Stebbing, F.R.S., F.L.S., said: Mr. President, may I be allowed for a few moments to intervene on behalf of those among us who may describe themselves as the know-nothing section of the audience, persons not a few who are committed to neither side in the controversy? When we return home and our friends gleefully enquire, "What then has been decided as to the Origin of Vertebrates?," so far we seem to have no reply ready, except that the disputants agreed on one single point, namely, that their opponents were all in the wrong. It occurs to me to illustrate the position by propounding another enigma. What is the origin of arguments? Take an example. Suppose a company in which some pedantic arithmetician asserts that two and three invariably make five. To those who like myself easily fall in with the views of the last speaker, the statement appears incontrovertible. But in some brains any positive declaration at once sets up what may be called an intellectual wriggle. This process soon enables the contradictory person to point out that two and three sometimes make six and sometimes minus one or plus one, as well as two-thirds of one or one and a half. Since one operation in arithmetic is as good as another, if not a great deal better, it follows that two and three do *not* invariably make five; far from it. Thus the wriggling of the brain originates argument.

Incidentally I may refer to two points raised by those who object to connecting the origin of Vertebrates with the Arthropoda. It was represented that the chitinous envelope of the latter was prohibitive of cilia. The delicate auditory cilia of Crustaceans are well known to carcinologists, but I am warned by intelligible signals that the term *cilia* is variously applied in different branches of Natural History. Another objection was founded on the difficulty of believing in the transfer of function from one organ to another, as required by Dr. Gaskell's hypothesis. But on this head the ingenuity of Nature seems to have been signally vindicated by the late Professor Gegenbaur, who showed how one part of an animal organism, in proportion as it went out of service for one function, could be appropriated for another.

Now, on the general question we have admired Dr. Smith Woodward's interesting account of the earliest fossil fishes. But these are accepted Vertebrates. For the origin of Vertebrates we must go back to something that is not a Vertebrate, such as may have existed perhaps far back in the Laurentian period. Imagine some soft, more or less elongated, animal organism wriggling about in the primeval sea. Then, as now, the hard conditions of the World demanded some sort of hardening on the part of living creatures. Some would find advantage in a stronger external coating, others in a strengthened central axis. But in either case the necessity of wriggling would often be paramount, giving rise on the one hand to a segmented exoskeleton, on the other to a jointed backbone. In these wrigglers, Mr. President, you have the origin of the Vertebrates,—a theory which it will be difficult to refute, as the supposed animals have hitherto revealed absolutely no relics.

The President having called upon Dr. Gaskell to reply, that gentleman said:—

It is impossible for me in the short time at my disposal to deal thoroughly with all the speakers in the two days' discussion. I will, however, do what I can.

Prof. MacBride in his latest paper prefers, as he said many years ago, to attribute my explanation to my diabolical ingenuity. As I have stated in my book, there is absolutely no ingenuity on my part; given the one fixed point that the infundibulum represents the old œsophagus and the animal remains upright, all the resemblances between the two groups of animals to which I have drawn attention, naturally follow. The devil is not in my ingenuity but in Nature's facts. I can sympathize with MacBride, for surely there could not be a more diabolical trick than to create from a lowly organised unsegmented animal whole groups of animals becoming more and more segmented, all characterised by the presence of an alimentary canal ventral to the nervous system, and then wipe them off the face of the earth, so that no trace of this sequence of forms is left among living animals. Not content

with this, this diabolic agency has left as the end result a segmented animal—the Vertebrate—in which with the greatest cunning he has not only made the supra-infundibular brain the exact counterpart of the supra-œsophageal and the infra-infundibular of the infra-œsophageal, but has grouped that nervous system round a large epithelial bag, which has nothing to do with a nervous system, but most ingeniously has been put in the exact position of the cephalic stomach and œsophagus of the Arthropod animal. To complete the story and give it an artistic finish, this ingenious devil plants above the brain of the Vertebrate impostor two median eyes exactly in the position of the two median eyes of the Palæostracan. He does not put them there for the purposes of sight, for they are functionless and degenerate in all Vertebrates, but just for sheer mischief, and how he must have chuckled over the happy thought of making them partly degenerate in the lowest Vertebrates, for he well knew that in the *Limulus* and his contemporaries they were already markedly degenerate and that they were no longer the chief eyes but their place had been taken by the large lateral eyes.

Prof. MacBride has asserted again, without giving instances, the statement so often made before, that I assume violent changes of function. Again and again I have denied it, and shown that I do not assume any such thing. Yet again I will go through the list of resemblances and ask where this statement of MacBride's is justified. The function and structure of the supra-infundibular brain is the same as that of the supra-œsophageal ganglia; the two lateral eyes and the two median eyes are the same in the two groups; the median nose has the same structure, the same nerves, and the same olfactory glomeruli in the two groups and even the slight difference, that the nasal tube in *Ammocœtes* opens dorsally and the olfactory passage in the Scorpion ventrally, vanishes after von Kupffer's demonstration that this *Ammocœtes* nasal tube originates as the tube of the hypophysis, which opens ventrally, and the dorsal position is due simply to the growth of the upper lip. Passing to the infra-œsophageal region, in both animals the anterior part is devoted to the organs of mastication and the posterior part to the organs of respiration; there is no change of function here, and I have given the evidence to show how the actual masticating and respiratory organs of the one group have insensibly shifted into those of the other group. Where are the violent changes of function so far? Then, if we pass into the spinal cord region, are we to look for them in the muscles or in the excretory organs or in the cœlomic cavities? Why, the whole evidence is that they are the same in the two groups; no sign of change violent or otherwise. I wonder what Prof. MacBride means. Surely this scathing indictment is not based on the thyroid gland which, I must repeat yet again, is not a mucin secreting gland but is a gland of great importance to the well being of the Vertebrate, apparently having something to do with

the manipulation of iodine. Is anything known of the function of the corresponding gland in the Scorpion? It may have the same function for aught I know. No! The only part of my theory which causes this assertion is that I have had the audacity to make a new gut and so go contrary to the laws of the germ-layer theory; I am content to leave it at that: time will show, I firmly believe, that the germ-layer theory is absolutely dead.

I come now to the observations of Goodrich; he as well as MacBride seemed, to my astonishment, to hold the view that *Amphioxus* was on the direct line of ascent to the Cyclostomes, that between *Amphioxus* and the Cyclostomes a brain had been developed with organs of sense, the eyes and nose. Surely this is a unique position! All other morphologists look upon *Amphioxus* as a degenerate animal, and degenerate in this precise direction. What conception has Goodrich of the evolutionary process, of the struggle for existence, of the survival of the fittest? Just consider it: here is a wretched animal without brains, without eyes, without a nose, victorious in the struggle for existence over the whole of the Invertebrate world. What is the driving force; how could it have taken place? Only, it seems to me, by some beneficent power taking special charge of him and assisting him in the growth of brain and of eyes and nose.

If there is one thing certain, surely it is Gegenbaur's dictum that the brain part is older than the spinal part, and further, the study of neurology shows clearly that in all animals, whether vertebrate or invertebrate, the brain is built up in connection with the optic and olfactory senses. No, the *Amphioxus* is not the ancestor of the Cyclostomes but, in my opinion, is closely related to the Cyclostomes as seen by its myomeres and the whole of the spinal region. After the Vertebrates had been well established the *Amphioxus*, in my opinion, arose by a process of degeneration from some ancestor of the Cyclostomes. Goodrich asserts that such a view is impossible, as no trace is seen in the development of the missing organs. Surely that argument is not good enough, for in the Tunicates, where a relationship with the Vertebrates is inferred from their development, such development is only found in certain members of the group and not in all.

Smith Woodward gave us an interesting discourse on certain early fishes, but I did not gather whether he thought the evidence I had brought forward pointed to the Osteostraci being Cyclostomes, though I think he favours that view. He called *Birkenia*, *Lasthenia*, and *Thelodus* Ostracoderms, and seemed to imply they were of the nature of Elasmobranchs. I cannot see why he called these scanty remains Ostracoderms, and would like to know whether, in his opinion, they were gnathostomatous, for the evidence is strongly in favour of the true Ostracoderms being cyclostomatous. In any case I see no difficulty in the presence of these forms, for surely it was likely enough that in the Upper Silurian seas some fish-like forms should have already progressed

onwards in the Elasmobranch direction with shagreen scales and possibly jaws from the primitive agnathous condition. The question of the interpretation of the lateral markings on some of the head shields of these mailed fishes is a comparatively small matter. Smith Woodward agrees with me that they show the presence of segmentation in this region, but thinks they were branchial segments; in my opinion, judging from Ammocœtes, they extend too far forward for branchiæ, and I think they are more likely to have been due to the presence of muscles supplied by the trigeminal nerve.

Coming to Lankester's speech I have a difficulty in finding anything to answer in it; he spoke of cryptograms and of Bacon and Shakespeare; another suggestion akin to the diabolic ingenuity of MacBride which hardly requires any further answer than I have given. He said there was no resemblance between the lateral eyes of Vertebrates and Arthropods, but that is not the point; it is not the dioptric apparatus upon which I was laying stress, but the retinal arrangements. It was the resemblance between this latter apparatus in the two groups upon which every observer from Berger to Parker has laid stress.

Finally, I come to the remarks of Dendy. He referred to the drawing of the right pineal eye of *Ammocœtes* as drawn in my book as a diagram. That is not so: the left half of the drawing is from the actual specimen, the right half is my interpretation of the meaning of the appearance seen. In my paper in the Q. J. Micr. Science all the drawings are carefully drawn by Wilson from the actual specimens and are not in any way diagrams. He referred to the finding by Studnička in the pineal eye of Ammocœtes of certain cells which he called ganglion cells. They are not arranged like an optic ganglion and are much more like the cells described in the median eye of *Limulus* by Lankester and Bourne, and called by them intrusive connective tissue cells. What these cells are I do not venture to assert; in any case they are present both in the median eye of *Limulus* and of Ammocœtes. As to *Geotria*, I have explained in my book that the cells grouped round the atrium may be nerve-cells as asserted by Dendy, but they are found along the nerve from the *ganglion habenulæ* to the eye. In the left eye of *Ammocœtes* the nerve has vanished and cells of the *ganglion habenulæ* run right into the eye. It is perfectly possible that *Geotria* represents an intermediate stage of degeneration between that of the right and left eyes of Ammocœtes, especially seeing that a portion of the original cavity is cut off to form the atrium by the massing of the cells in question. As to the tube of the nervous system, Dendy, as well as all the other speakers on that side, find it very convenient to leave out the infundibular prolongation in their picture of the formation of an epithelial tube, an unfortunate omission as it happens to be the main point of my argument. Dendy's view that the choroid

plexuses form a respiratory organ for the brain is novel: I wonder what Dendy's conception of a respiratory organ is.

In conclusion, I am grateful to the Linnean Society for allowing me to put my views before them, and only hope that all those who dissent from them will study for themselves organ by organ the resemblances between the two groups of animals and make up their minds whether they are accidental or, as I believe significant of a real relationship.

The PRESIDENT said that at that hour of the evening, and after so brilliant a discussion, no one would expect a speech from a botanical Chairman, though much had been said of great general interest to all biologists. On the first evening Dr. Gaskell had directly appealed to the Chair with reference to his belief that "each higher group of animals has arisen in succession from the highest race developed up to that time." At present he would only say that the evidence on the botanical side appeared not unfavourable to such a view; perhaps he might have an opportunity of returning to this question on the 24th of May.

The President felt that any criticisms of his on the course of the discussion might well be dispensed with, for he had been anticipated by Prof. Stanley Gardiner, whose remarks appeared to him to agree, point for point, with those which would occur to the mind of any present-day botanist in listening to the discussion.

It only remained for him to ask the Fellows to return their hearty thanks to Dr. Gaskell and all who had taken part in the discussion, for the intellectual entertainment they had provided.